

A NEW GENUS OF FOSSIL PUFFERFISH
(TETRAODONTIDAE: TETRAODONTIFORMES) BASED
ON A NEW SPECIES FROM THE OLIGOCENE OF
RUSSIA AND A REFERRED SPECIES FROM
THE MIOCENE OF UKRAINE

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Abstract.—A new genus of tetraodontid pufferfish, *Archaeotetraodon*, is proposed for two fossil species with uniquely specialized bifurcate scale spinules: *winterbottomi*, a new species based on ten specimens from the Oligocene of Russia in which nearly all of the spinules are bifurcate; and *jamestyleri* Bannikov (1990), based on two complete specimens and a fragment from the Miocene of Ukraine in which only two scales in the middle of the body have bifurcate upright spinules. An especially long rayless pterygiophore extending forward from the dorsal-fin origin in *Archaeotetraodon* (in *winterbottomi*; condition unknown in *jamestyleri*) is similar to that found in the Recent *Lagocephalus* but this feature cannot be unequivocally polarized and may not indicate relationship between these two genera.

Expeditions by the Paleontological Institute of the Russian Academy of Sciences to the North Caucasus have discovered a rich Lower Oligocene marine ichthyofauna in the Pshekhsky Horizon of the Lower Maikop deposits. This was first described by Danilchenko (1960), with further studies more recently by the second listed author and his cooperating colleagues. Among newly excavated fossils of early Oligocene age are ten specimens, four in counterpart plates, that are unique among tetraodontids by having most of the upright scale spinules that cover the entire body bifurcate from the base and divergent distally. The bifurcate scale condition is shown to be a specialization because all Recent and one of the other fossil tetraodontids as well as all members of the diodontid sister group have undivided upright scale spinules. We describe these specimens as a new species and type of a new genus: *Archaeotetraodon winterbottomi*.

Our re-examination of the scales in materials of all previously described fossil tetraodontids based on relatively entire specimens shows that one of them, *Sphoeroides jamestyleri* Bannikov (1990), from the Miocene of Ukraine, has most of the scales with unbranched spinules but that a limited patch in the middle of the body has bifurcate spinules. We transfer *S. jamestyleri* from *Sphoeroides*, into which it was originally placed mostly for the convenience of not having to create a new genus, to *Archaeotetraodon* on the basis of its sharing with *A. winterbottomi* specialized bifurcate scales. The two species of *Archaeotetraodon* differ from one another not only in the coverage with bifurcate scales but also in several osteological features.

Methods

Length is standard length (SL) unless otherwise stated. Fossil materials are from the collections of the Paleontological Institute (PIN) of the Russian Academy of Sciences in Moscow, the Museo Civico di Storia Naturale di Verona (MCSNV), the Istituto di

Geologia della Università di Padova (IGUP), and Sammlung der Philosophie-theologie Hochschule der Eichstätt (SPHE). Comparative anatomical preparations and radiographs of Recent species of tetraodontiforms are those listed in Tyler (1980), supplemented by those of tetraodontids listed in Tyler et al. (1992).

In many derived groups of tetraodontiforms, including tetraodontids, there is a bony element in the upper midline of the body just in front of the soft dorsal fin that is thought to represent a basal pterygiophore that no longer bears dorsal-fin spines. This was called a supraneural in Tyler (1980), but is here referred to as a rayless pterygiophore, following the recommendation of Mabee (1988:836), who demonstrated that true supraneurals (predorsals) are not homologous with such pterygiophores.

For tetraodontoid phylogeny we follow the cladistic analysis of Winterbottom (1974) and the evolutionary systematics of Tyler (1980), which, respectively on the basis of specialized myological and osteological features, are in agreement that: diodontids are the sister group of tetraodontids; molids are the sister group of the tetraodontid + diodontid clade; triodontids are the sister group of the tetraodontid + diodontid + molid clade; and the Eocene eoplectids are the morphologically primitive sister group of all of these other tetraodontoids. Among other tetraodontiforms, the balistoid + ostracioid clade is the first outgroup and the triacanthoid clade the second outgroup.

There is no cladistic analysis available for the genera of tetraodontids, and Tyler (1980) simply placed the Recent genera into three groups of relative degrees of morphological specialization in what can be considered an unresolved trichotomy. The Eocene *Eotetraodon* was presumed in that work to be the morphologically primitive sister group of these three groups of Recent genera because of its retention of such plesiomorphic features as twelve principal caudal-fin rays and

pleural ribs (both of which are found in triodontids); however, because diodontids and molids have no pleural ribs and fewer than twelve caudal-fin rays, it is more parsimonious to propose that the twelve caudal-fin rays and pleural ribs of *Eotetraodon* are reversals.

Although it was inconsistent with his presumed phylogeny of tetraodontid genera, Tyler (1980) continued the practice of recognizing *Canthigaster* as subfamilially distinct from other tetraodontids even though the genus *Carinotetraodon* was shown to be anatomically intermediate between *Canthigaster* and other tetraodontids in many ways, including several specialized features (e.g., skin ridge-lifting behavior, highly arched vertebral column, large haemal spines on abdominal vertebrae). This led Tyler (1980) to the conclusion that *Carinotetraodon* and *Canthigaster* had a close common ancestry. Therefore, we agree with Winterbottom (1974:99) that *Canthigaster* cannot reasonably be recognized as subfamilially distinct from (and sister group to) a polyphyletic subfamily for all other tetraodontids, including *Carinotetraodon*. With the phylogeny of tetraodontid genera so poorly known, we compare any unusual features of *Archaeotetraodon* with comparable conditions in all other tetraodontid genera, including the specialized *Canthigaster* + *Carinotetraodon* clade to which we doubt *Archaeotetraodon* is closely related.

Family Tetraodontidae (sensu Tyler, 1980)
Archaeotetraodon, new genus

Type species. — *Archaeotetraodon winterbottomi*, new species, by present designation; other species, *Sphoeroides jamestyleri* Bannikov (1990), by referral herein.

Diagnosis. — Differs from all other tetraodontids by the presence of bifurcate upright spinules on either most of the scale plates over the entire body (in *winterbottomi*) or on many of those of the middle of the body (in *jamestyleri*).

Description. — With the exception of a few species in which scales have been secondarily lost (several species of both *Sphoeroides* and *Takifugu* and single species of both *Lagocephalus* and *Tetraodon*; Tyler 1980:297–298) all Recent tetraodontids have specialized scales in which the basal plate, which has two or more processes radiating out into the skin, bears an upright spinule that protrudes through the skin as a prickle. The spinule is of varying stoutness and length, but most often is short and slender (in contrast to the larger and stouter projecting spines in diodontids), giving a shagreen-like quality to the skin (see illustrations of scales in Recent species of numerous tetraodontid genera in Tyler 1980: 291–297).

That the new species of tetraodontid from the Oligocene, *A. winterbottomi*, has an extensive covering of bifurcate scale spinules led us to re-examine the scales in the two previously described species of fossil tetraodontids based on relatively entire specimens, the Eocene *Eotetraodon pygmaeus* (Zigno 1887) and the Miocene *Sphoeroides jamestyleri* Bannikov (1990). The holotype and four other previously unreported specimens of *E. pygmaeus* are covered with unbranched spinules like those of all Recent tetraodontids. The holotype of *Sphoeroides jamestyleri* does not have the scales preserved, but the paratypic entire specimen has a complete covering of scales, most of which have unbranched spinules. However, some scales in the middle of the body (it is impossible to distinguish whether this is dorsal, ventral, or lateral) are just as distinctly bifurcate distally as those in *A. winterbottomi*, although the spinules are proportionally shorter in *S. jamestyleri*.

Because all species, both fossil and Recent, of the diodontid sister group have scale plates with unbranched upright spinules or spines like those of all Recent and one of the fossil species of tetraodontids (except more massive), we propose that spinules with undivided upright shafts are primitive

for the tetraodontid + diodontid clade and that the deeply bifurcate spinules in the Oligocene *A. winterbottomi* and Miocene *S. jamestyleri* are a specialization. Therefore, the bifurcate spinule condition is a synapomorphy of *A. winterbottomi* and *S. jamestyleri*. The latter was originally placed in *Sphoeroides* because it is thought to be a morphologically relatively primitive genus (Tyler 1980) defined by a combination of what seem to be mostly plesiomorphic features, and no features that are known to be specialized. It was simply convenient to place *S. jamestyleri* in that poorly defined genus pending acquisition of better preserved materials showing more internal features which might clarify its relationships, but such materials are not yet available. However, we can state that all of the few known internal features of similarity between *S. jamestyleri* and the species of *Sphoeroides* are plesiomorphic (e.g., moderate interorbital and ethmoid widths; moderate and mostly laterally directed extensions of the lateral ethmoids, sphenotics, and pterotics) and that there are no known specialized features of similarity that unite *S. jamestyleri* with *Sphoeroides*. Because *S. jamestyleri* does share the uniquely derived feature of bifurcate scale spinules with *A. winterbottomi*, we remove *jamestyleri* from *Sphoeroides* and place it in *Archaeotetraodon* along with *winterbottomi*.

We note that in molids the basal plates of the scales are rounded to rectilinear and bear a central emargination or low spinule, and in at least smaller specimens of *Mola* some of these spinules are branched distally (see illustration in Tyler 1980:369). In all other tetraodontoids with upright spinules on the basal plate, the spinules are unbranched (a single spinule in eoplectids, the sister group of all other tetraodontoids, and several spinules in the poorly known zig-noichthyids, that are most closely related to the tetraodontid + diodontid clade). In triodontids the scales bear a low spiny ridge and there are no upright spinules. There-

fore, on the basis of the phylogeny of tetraodontoid families proposed by both Winterbottom (1974) and Tyler (1980), it is most parsimonious to presume that the distally branched spinules in some molids and the deeply bifurcate branched spinules in *Archaeotetraodon* are independent acquisitions.

Etymology.—From the Greek: *archaios*, old or ancient, and *tetraodon*, for the four tooth plates characteristic of the family Tetraodontidae; masculine.

Similarities of *Archaeotetraodon* to Other Tetraodontids

Rayless pterygiophore.—*Archaeotetraodon winterbottomi* has an exceptionally long rayless pterygiophore, averaging 18% SL as measured from the anterior end of the element to the anterior end of the base of the soft dorsal fin in the three specimens in which this region is preserved. We presume that this long slender element is a single piece of bone from its posterior end at the dorsal-fin origin to its anterior end at the level of the vertical through the centrum of the sixth to seventh abdominal vertebra because we cannot see any interruptions or articulations in it, although our view of the bone is somewhat obscured by the layer of spiny scales in the overlying skin. In the holotype of *A. jamestyleri* the region anterior to the dorsal fin is poorly preserved, while in the paratypic entire specimen the skeleton is much disarticulated and it is not possible to recognize a rayless pterygiophore among the mixture of bones. Thus, the condition of the rayless pterygiophore in *A. jamestyleri* is unknown and in the following discussion of the rayless pterygiophore the statements about *Archaeotetraodon* are based on the conditions in *A. winterbottomi*.

In some Recent tetraodontids with relatively long rayless pterygiophores, this element does not reach posteriorly to the dorsal-fin origin but, rather, terminates anterior

to it and articulates there with an anterior process on the distal end of the first basal pterygiophore of the dorsal fin. We see no evidence of such an anterior process on the first basal pterygiophore in *Archaeotetraodon*, but that pterygiophore is not well exposed in our material. Although we cannot be absolutely sure of it, we have no reason to believe that the rayless pterygiophore in *Archaeotetraodon* does not extend as a single slender bone for the full length of the distance from its anterior end to the dorsal-fin origin. Nevertheless, it is possible that some small portion of our measurement of the rayless pterygiophore posteriorly in *Archaeotetraodon* may include part of the distal head of the first basal pterygiophore of the dorsal fin. Even with that caveat, we believe that the average measurement of 18% SL is a fair estimate of the length of the rayless pterygiophore in *Archaeotetraodon*. No other tetraodontid has a rayless pterygiophore as long as that in *Archaeotetraodon*, but a few genera contain species with rayless pterygiophores almost as long.

The rayless pterygiophore is especially long and slender in the six species of *Lagocephalus* examined, more so in some species than in others. For example, in *L. inermis* (Temminck & Schlegel), *L. laevigatus* (Linnaeus), *L. lunaris* (Bloch & Schneider), and *L. spadiceus* (Richardson) the rayless pterygiophore length averages 8–9% SL (in 2 to 12 specimens of each species examined), while it averages 12% SL in *L. scleratus* (Gmelin) (in 4 specimens) and 15% SL in *L. lagocephalus* (Linnaeus) (in 2 specimens), the latter being the longest rayless pterygiophore of which we are aware among Recent tetraodontids. In all of these species of *Lagocephalus* the distal end of the first dorsal-fin basal pterygiophore has a prominent anterior process to which the rayless pterygiophore articulates. The rayless pterygiophore of *Lagocephalus*, even though shorter than in *Archaeotetraodon*, extends at least as far forward as in *Archaeotetraodon*, and, in *L. lagocephalus*, extends even

further forward, to the level of the vertical through the region of articulation between the centra of the fourth and fifth abdominal vertebrae. The two species of *Lagocephalus* with the longest rayless pterygiophores, *L. scleratus* and *L. lagocephalus*, are streamlined in form and have an offshore pelagic habitat; there may be a correlation in tetraodontids between a long and slender rayless pterygiophore and a strong swimming, pelagic mode of life.

The rayless pterygiophore is relatively long in the nine species of *Canthigaster* examined, averaging between 9% and 13% SL. The rayless pterygiophore of *Canthigaster* differs from the slender rod as found in *Archaeotetraodon* and *Lagocephalus* in being heavier, deeper, concave ventrally, and curved ventrally at its anterior end, following the contour of the arched back.

In most species of *Sphoeroides* the rayless pterygiophore is short, averaging about 4–5% SL, but the element is somewhat longer in such species as *S. spengleri* (Bloch) and *S. marmoratus* (Lowe), averaging 6–7% SL. In *S. formosus* (Gunther) (sometimes recognized in the monotypic *Guentheridia*) the rayless pterygiophore is far longer, heavier, and deeper than in the other species of *Sphoeroides*, averaging 12% SL (in 5 specimens) but without the slender form found in *Lagocephalus* and *Archaeotetraodon*.

Other than the species mentioned above, we know of no other tetraodontids with notably long rayless pterygiophores, i.e., of 10% SL or greater length. The condition of the rayless pterygiophore in a variety of tetraodontids can be assessed from the illustrations of representative species in Tyler (1980:figs. 195, 203, 226–244), including its absence in a few species.

The similarity in the length of the long, slender rayless pterygiophore between *Archaeotetraodon* and some species of *Lagocephalus* is difficult to interpret because of the unknown phylogeny within tetraodontids and because diodontids, their sister group, do not have a rayless pterygiophore.

In the molid sister group of the tetraodontid + diodontid clade the rayless pterygiophore is either present as a short deep piece (*Mola*), absent or fused with the first basal pterygiophore of the soft dorsal fin (*Masturus*), or perhaps consolidated into a long complex structure that connects the first basal pterygiophore of the soft dorsal fin with the supraoccipital crest (*Ranzania*). In triodontids a rudimentary spiny dorsal fin, when present, of two or three spines is borne on two basal pterygiophores that are connected to the basal pterygiophores of the soft dorsal fin by two short rayless elements. These two short elements presumably are derived from basal pterygiophores that no longer support spines at the rear of the rudimentary spiny dorsal fin. In those populations (Indian Ocean) of *Triodon macropterus* (Lesson) (the only Recent representative of the family) that usually entirely lack the spiny dorsal fin, all four of the elements in this series that extends anteriorly from the soft dorsal-fin origin therefore are rayless pterygiophores, the first of which is elongate and the more posterior three pieces short. In eoplectids a well-developed spiny dorsal fin is present and its basal pterygiophores connect with those of the soft dorsal fin without the intervention of rayless pterygiophores. Among the outgroup tetraodontiforms, the six dorsal-fin spines in triacanthoids are borne on four or five basal pterygiophores and there are no rayless pterygiophores between the basal pterygiophores of the spiny and soft dorsal fins. In balistids the three dorsal-fin spines are borne on two basal pterygiophores that form a complex carina supported by a rayless pterygial strut that braces the carina against the first basal pterygiophore of the soft dorsal fin, with the strut apparently being derived from the third basal pterygiophore of the spiny dorsal fin of triacanthoids. In monacanthids there are two dorsal-fin spines, and the less robust carina, which is formed from a single basal pterygiophore, is not supported posteriorly by a pterygial strut. In ostracioids the spiny dor-

sal fin is absent and a long and deep (aracanids) or short (ostraciids) rayless pterygiophore is present anterior to the base of the soft dorsal fin. Thus, when the spiny dorsal fin is absent in tetraodontiforms such as ostraciids, rayless pterygiophores are present and apparently represent basal pterygiophores of the absent spiny dorsal fin, while the reduction in number of dorsal-fin spines and their supporting basal pterygiophores from posteriorly in the series in balistids in comparison to triacanthoids is accompanied by the apparent conversion of the third basal pterygiophore of triacanthoids into the rayless pterygial strut of balistids.

Most germane, however, is the situation in triodontids, the sister group of all other Recent families of tetraodontoids, in which the distinction between basal pterygiophores and rayless pterygiophores depends simply on whether the rudimentary dorsal-fin spines are present or not. Therefore, we propose that the presence of a rayless pterygiophore, representing a rudimentary support of the now absent spiny dorsal fin, is primitive for the tetraodontid + diodontid + molid clade of tetraodontoids. However, it is equally parsimonious to hypothesize that: 1) a rayless pterygiophore was present in the ancestor of the tetraodontid + diodontid clade and that the rayless pterygiophore was independently lost by all diodontids and by some tetraodontids; or 2) a rayless pterygiophore was lost in the ancestor of the tetraodontid + diodontid clade and the rayless pterygiophore acquired by most tetraodontids as a reversal to the ancestral tetraodontoid condition. Moreover, even given that a rayless pterygiophore is primitive for the tetraodontid + diodontid + molid clade, it is not known whether that element was long or short or slender or stout. Presuming that the rayless pterygiophore of the ancestral tetraodontoid without a spiny dorsal fin was one of the four dorsal pterygial elements as found in triodontids, it could as logically be the long, stout, anteriormost first rayless pte-

rygiophore of those *Triodon macropterus* lacking dorsal-fin spines as it could be one of the three short and heavy more posterior rayless elements. We have no way of knowing at present whether the rayless pterygiophore in the ancestral tetraodontoid without a spiny dorsal fin was long or short. Therefore, similarity in the long rayless pterygiophore of *Archaeotetraodon* and *Lagocephalus* may be plesiomorphic and not indicative of relationship.

Our surmise is that the great length and, especially, the slender form of the rayless pterygiophore is a derived feature, but since we do not know of any unequivocally derived features shared by *Archaeotetraodon* and *Lagocephalus*, it may be that the putatively derived condition of the long, slender rayless pterygiophore is independently acquired by these two genera. From what little is known of its osteology, *Archaeotetraodon* differs from *Lagocephalus* in having relatively evenly tapered neural and haemal spines on the vertebrae of the caudal peduncle anterior to the penultimate vertebra, whereas in *Lagocephalus* these are expanded anteroposteriorly, a derived condition (absent in other tetraodontids and in all other tetraodontoids).

Elongate head spines.—In at least one specimen of *Archaeotetraodon winterbottomi* the spinules on the top of the head are longer than elsewhere and many of these are not bifurcate. In only one other species of tetraodontid are the spinules on the head much longer than those on the body, this being one of the several species of *Amblyrhynchotes*, *A. piosae*. In *A. piosae* the body is made exceptionally prickly by spinules that are longer than in other tetraodontids, and the spinules on the top and side of the front of the head are especially elongate, up to 8% SL. These spinules are proportionally far longer than those that are slightly elongate on the top of the head in *A. winterbottomi*. In both cases among tetraodontids in which speciose genera have a few species in which spiny scales are lost, these species are

not considered to be closely related within their respective genera (*Sphoeroides* and *Takifugu*) and the loss of spines has been considered to be independent (Tyler 1980: 297). With so much homoplasy in even the presence or absence of spines within tetraodontid genera, we place no phylogenetic significance on the fact that both one specimen of *A. winterbottomi* and one of the several species of *Amblyrhynchotes* have the spinules longer on the head than elsewhere, especially when the spinules in *A. winterbottomi* are otherwise so different (shorter and bifurcate) than those in *A. piosae*, and when there are no other derived features of similarity between *Archaeotetraodon* and any of the species of *Amblyrhynchotes*. *Archaeotetraodon* differs from *Amblyrhynchotes* not only by its short bifurcate scales but most notably also by having 18 versus 19 or 20 vertebrae (in the three species of *Amblyrhynchotes* examined) and a long (18% SL) versus short rayless pterygiophore (5–6% SL in three species of *Amblyrhynchotes*).

Generic Relationships

On the basis of its few known osteological and external features we are not able to place *Archaeotetraodon* into one of the three morphological groups recognized by Tyler (1980) for Recent genera of tetraodontids. Likewise, we do not find any special similarity between the two species of *Archaeotetraodon* and other fossil species of tetraodontids. The Eocene *Eotetraodon pygmaeus* (Zigno) has neither bifurcate scales nor a long rayless pterygiophore. The Pliocene *Sphoeroides hyperostosis* (Tyler et al. 1992) is based on skulls and anterior vertebrae but the scales and portions of the body that might include a rayless pterygiophore are unknown; it differs from *Archaeotetraodon* by the extensive hyperostosis of many skull bones at sizes as small as that of the larger specimens of either of the two species of *Archaeotetraodon*. Several other species of fossil tetraodontids have been named on the

basis of pieces of jaw bones of Miocene and younger age but these cannot be usefully compared with the fossil species based on more complete specimens.

We can only call attention to the unique bifurcate scales that distinguish *Archaeotetraodon* from all other genera of tetraodontids and note that while the elongate and slender rayless pterygiophore as found in *A. winterbottomi* and some *Lagocephalus* may be a specialization for a pelagic mode of life, it seems likely to have been an independent acquisition in the few pelagic species of *Lagocephalus* and in *A. winterbottomi*, which has been found in a predominantly pelagic fossil ichthyofaunal assemblage.

Archaeotetraodon winterbottomi, new species Figs. 1–4

Diagnosis. — *Archaeotetraodon winterbottomi* differs from the only other species of the genus, *A. jamestyleri*, by having: a vertebral formula of 8+10 (versus 7+11 in *jamestyleri*); almost complete covering of bifurcate scale spinules (versus bifurcate only on middle of body); haemal spine of penultimate vertebra with a moderately long posteroventral process under the parhypural region (versus no prolongation); supraclithrum relatively long and narrow (versus shorter and thicker).

Description. — Body moderately elongate (Figs. 1–2). Vertebrae 18 in four specimens in which total number can be counted, with eight abdominal and ten caudal in only specimen (holotype) in which proximal end of first anal-fin basal pterygiophore can be seen in association with a haemal spine; vertebral column relatively straight, only gently arched in abdominal region. Caudal skeleton relatively distinct in holotype, and having normal tetraodontid pattern of a long parhypural, a lower hypural plate fused to last centrum, an upper free hypural plate and an epural (exact shape unclear) above last centrum. Penultimate vertebra (PU₂)

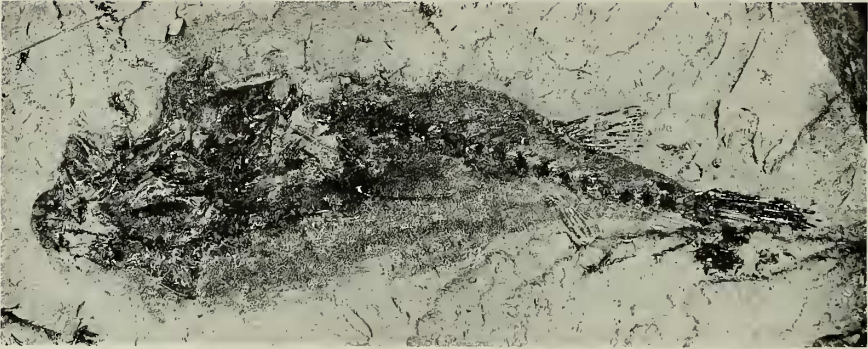


Fig. 1. Photograph of holotype of *Archaeotetraodon winterbottomi*, PIN 3363/111, 90.0 mm SL, Lower Oligocene (Maikopian) of North Caucasus, southwest Russia.

with broad neural and haemal spines, the latter prolonged posteriorly under a little more than half of length of parhypural; more anterior caudal vertebrae with more slender neural and haemal spines, except haemal spines of first three caudal vertebrae short, where proximal ends of anal-fin basal pterygiophores are supported. First three abdominal vertebrae apparently with bifid neural spines and fourth abdominal vertebra with neural spine bifid anteriorly but undivided posteriorly, where it is prolonged posteriorly over base of neural spine of fifth vertebra.

Dorsal-fin rays nine in two specimens and nine or perhaps ten in one specimen. Anal-fin rays eight in only specimen in which all rays are preserved, at least basally. Basal

pterygiophores in dorsal fin seven and in anal fin six in single specimen in which these can be counted. Caudal-fin rays 11 in four specimens, best preserved in holotype, with uppermost ray and two lowermost rays unbranched and other eight rays branched, four above middle of hypural plate and four below (typical tetraodontid condition). Caudal-fin length 23.3–27.3% SL (25.8% average) in three specimens. Pectoral fin not well enough preserved to describe.

A single upright spinule arising from each basal scale plate, spinules mostly short and divergently bifurcate from base (Fig. 3), length of upright spinules along top of middle of body in nine specimens 0.7–1.6% SL (1.3% average); these prickly scales present continuously over most of head and body.

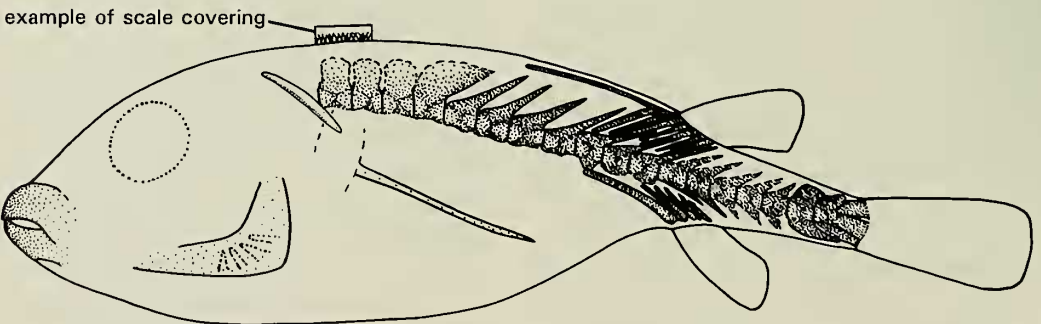


Fig. 2. Reconstruction of *Archaeotetraodon winterbottomi*, based on the holotype, data as in Fig. 1.

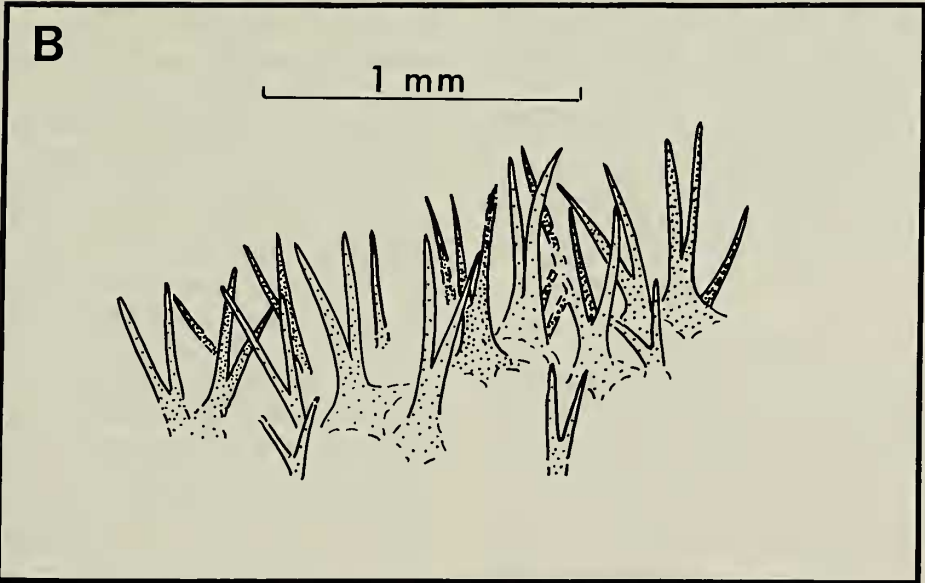


Fig. 3. A. Photograph of scales along dorsal surface of paratype of *Archaeotetraodon winterbottomi*, PIN 3363/115, ca. 40 mm SL, longest upright bifurcate spinules 0.5 mm (1.3% SL), age and locality as in Fig. 1. B. Drawing of selected scales along same dorsal surface as in A.

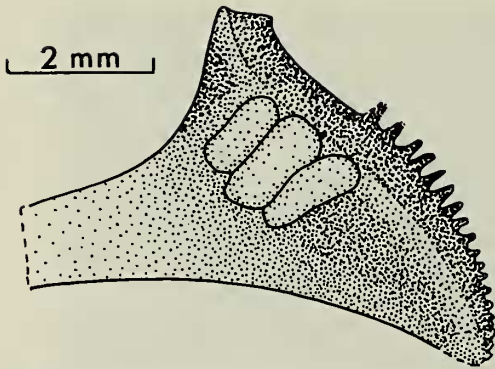


Fig. 4. Drawing of inner surface of premaxilla of holotype of *Archaeotetraodon winterbottomi*, data as in Fig. 1.

In one specimen (PIN 3363/120) a small group of about ten spinules on top of head slightly longer than those on body (1.4% versus 0.9% SL) and mostly unbranched, with all other spinules on head and body bifurcate; we presume that having a few slightly elongate and non-bifurcate spinules on top of head is normal for at least some specimens of this species (perhaps a sexually dimorphic feature).

Rayless pterygiophore long and slender, apparently a single piece, its posterior end at origin of soft-dorsal fin and its anterior end at level of vertical through centrum of sixth or seventh abdominal vertebra; its length 16.0–20.6% SL (18.1% average) in three specimens.

Inner surface of premaxilla visible in two specimens, both of which have three trituration teeth, about three times as mediolaterally wide as anteroposteriorly deep; medial edge of premaxilla with articular processes increasing in size posteriorly in series (Fig. 4), interdigitating with similar processes on apposed premaxilla. Inner surface of dentary visible in one specimen and no trituration teeth present; medial edge of dentary with articular processes like those of premaxilla.

Preopercle broad and strongly curved, with ridges in middle region. Postcleithrum long and slender. Supracleithrum long and

gently curved, with a low medial flange. Interorbital width moderate, least width about 4.0–4.5% SL in two entire specimens in which it is possible to recognize the lateral edges of the upper orbit in neurocrania preserved in dorsoventral view. No other features of skeleton clearly enough exposed or preserved to warrant description.

Etymology.—*winterbottomi*, honoring our friend and colleague Richard Winterbottom, Royal Ontario Museum, in recognition of the excellence of his important studies on the phylogeny of tetraodontiforms and of his great help to us in our own efforts with the plectognath fishes.

Type materials.—Holotype: PIN 3363/111 (head to left) and 111a, counterpart plates, River Pshekha, 90.0 mm SL. Paratypes: PIN 3363/112 (head to right), single plate, River Belaya, 53.9 mm SL; PIN 3363/113 (head to left), single plate, River Belaya, 36.5 mm SL; PIN 3363/114 (head to left) and 114a, counterpart plates, River Belaya, 27.8 mm SL; PIN 3363/115 (dorsoventral impression), single plate, River Belaya, ca. 40 mm SL; PIN 3363/116 (head to left), single plate, River Kuban, most of head missing, length of vertebral column 32.6 mm; PIN 3363/117 (head to left), single plate, River Pshekha, fragment of most of vertebral column, whose length is ca. 33 mm; PIN 3363/118 and 118a (dorsoventral impression), counterpart plates, River Belaya, 24.7 mm SL; PIN 3363/119 (head to left) and 119a, counterpart plates, River Belaya, 52.1 mm SL; PIN 3363/120 (head to right), single plate, River Belaya, 64.2 mm SL. Except for the two specimens preserved entirely as dorsoventral impressions, all of the above are preserved as lateral impressions of the body in which, however, the neurocranium is often in dorsoventral view.

Type locality.—Holotype from River Pshekha (at Gorny Luch). Paratypes from Rivers Pshekha, Belaya (upstream from the settlement of Abadzekhskaya), and Kuban (near the town of Cherkessk), all of which sites are within, respectively, 32 and 150

km of one another in the Pshekhsky (Pshekha) Horizon, lower part of the Maikop (Maikopian) deposits, Lower Khadum Formation, Lower Oligocene, North Caucasus of southwest Russia, about 35 million years ago.

Stratigraphy and ichthyofaunal associations.—About 55 other species of fishes have been collected at the localities where the type series of *A. winterbottomi* were found in the Maikop deposits of the Lower Oligocene. These fishes are predominantly pelagic forms (see table 3 in Danilchenko 1980), including the *Caprovesposus acronurus* presettlement stage of an acanthurid (Bannikov & Tyler 1992), numerous clupeids of the genera *Sardinella* and *Pomolobus* and gadids of the genus *Palaeogadus*. Several strata of the Pshekhsky Horizon bear rather numerous mesopelagic photophore-bearing fishes of the genera *Eomyctophum*, *Vinciguerria* and *Scopeloides*. Moreover, representatives of such apparently pelagic families as Scombridae (*Scombrosarda*, *Sarda*), Trichiuridae (*Lepidopus*), Palaeorhynchidae (*Palaeorhynchus*, *Homorhynchus*), Nomeidae (*Psenicubiceps*, *Rybapina*), Stromateidae (*Pinichthys*), etc., were abundant in the early Eocene of the North Caucasus. Coastal and benthic fishes were much rarer, although among those few benthic species is the only previously known Maikopian tetraodontiform, *Oligobalistes robustus* Danilchenko (1960).

We presume that the preponderance of pelagic fishes at the localities of the type series of *A. winterbottomi* is evidence that it is an offshore or pelagic species of tetraodontid, like some of the species of *Lagocephalus*.

The gray, flaky marls and calcareous clays of the Oligocene Pshekhsky Horizon cover light calcareous rocks of the underlying Upper Eocene Byeloglinsky Horizon of the North Caucasus. The only fish remains that are known from the latter horizon are isolated scales of a large elopiform of the genus *Lyrolepis*.

Comparative Fossil Materials

Eotetraodon pygmaeus (Zigno 1887): all specimens from the Lower Eocene of Monte Bolca, Italy; IGUP 6890–91, counterpart plates, holotype, 18.2 mm SL; MCSNV T137–138, counterpart plates, 16.1 mm SL; MCSNV T139, single plate, 14.2 mm SL; SPHE 1970/48, single plate, 15.5 mm SL; SPHE 1970/47, single plate, 90.5 mm SL.

Archaeotetraodon jamestyleri (Bannikov 1990): all specimens from the Tarkhanian Horizon of the Lower Miocene at Kamyshlak, Kerch Peninsula, Crimea, Ukraine; PIN 287-9, counterpart plates, holotype, 22.6 mm SL; PIN 3974-8, single plate, paratype, vertebral column distorted, cranium preserved as dorsoventral impression of 16.4 mm length from anterior end of vomer to rear of occipital region, estimated 60 mm SL; PIN uncatalogued, fragment representing part of caudal peduncle.

Spherooides hyperostosus Tyler, Purdy, & Oliver (1992): both specimens from the Yorktown Formation of the Lower Pliocene of Lee Creek Mine, Beaufort County, North Carolina, USA; USNM 437601, relatively complete three dimensional skull and first four vertebrae, holotype, 72.5 mm cranium length; USNM 290643, three dimensional cranium, paratype, 37.0 mm cranium length.

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